

# The phylogenetic relationships of salmonoid fishes

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## Contents

Introduction .....	145
Taxonomic history .....	145
Materials and methods .....	146
Interrelationships of the Salmonidae .....	149
Proposed changes in taxonomic ranking .....	151
Acknowledgements .....	152
References .....	152

## Introduction

The family Salmonidae (salmons, trouts and charrs) have long been of scientific interest, primarily because of their economic significance but also because their phylogenetic relationships to other teleost groups have proved difficult to ascertain. As currently defined, the family comprises three subfamilies, *viz* Salmoninae (salmons and trouts), Thymallinae (graylings) and Coregoninae (charrs and white-fishes). The Salmonidae have been regarded as a relatively primitive teleost group since they have supposedly retained many features often associated with so-called 'primitive' groups. Such features include; soft fin-rays; adipose fin; oviducts absent or incomplete and three upturned caudal vertebrae. This view is perhaps misleading as the Salmonidae possess many unique characteristics particularly with regard to their physiology and reproductive strategies.

The Salmonidae are native throughout the Holarctic region but are absent from tropical and austral regions. Some species (e.g. *Salmo trutta* and *Oncorhynchus mykiss*) have, however, been introduced into these regions (Scott & Crossman, 1973:186). The original distribution of some salmonid species is difficult to establish as a result of extensive introductions (deliberate and accidental) which have expanded their natural ranges, a consequence of their economic importance.

The Salmoninae have both freshwater and anadromous representatives, while the Thymallinae are restricted to freshwater alone. All Coregoninae except *Coregonus oxyrhynchus* are also freshwater inhabitants.

All Salmonidae breed in freshwater. There are no strictly marine forms, or any that spawn in the sea. This feature has been used to support the hypothesis that they have a freshwater origin (Tchernavin, 1939:18).

Because of their economic significance the reproductive strategies of the Salmonidae have been the centre of much attention and an extensive volume of literature has accumulated on the subject (e.g. Shapovalov & Taft, 1954; Hartman, 1959; Frost & Brown, 1967; Carlander, 1969; and Havey &

Warner, 1970). A summary of this information is beyond the scope of this study.

The Salmonidae are generally carnivorous, and feed on a variety of freshwater and marine organisms. Food preferences vary according to size and development of the predator. The juveniles while in freshwater generally feed on insect larvae, but as adults, food items include a variety of fish and Crustacea (Dymond, 1963:482; Bănărescu, 1964). Most salmonids can be considered opportunistic feeders.

In spite of extensive biological and taxonomic literature concerning salmonid fishes, little attention has been given to the interrelationships of the included taxa. Some authors have presented phylogenetic speculations (see below for a full summary). However, these have been based primarily on *ad hoc* assumptions of how the taxa evolved. By means of a cladistic analysis (*sensu* Nelson & Platnick, 1981; and Patterson, 1982), this study set out to establish the intergeneric relationships of the Salmonidae using comparative osteology and myology.

This study also considers the question of outgroup relationships, as the interrelationships of the 'Salmoniformes' are in as much disarray as are the intrarelations.

## TAXONOMIC HISTORY

As discussed above, the intrarelations of the Salmonidae and indeed the 'Salmoniformes' is the source of much confusion and is still in a state of flux.

Early ichthyologists, not concerned with lower level relationships, grouped together the salmonid taxa with little consideration for their intrarelations. Early classifications (e.g. Regan, 1913:289) put the Salmonidae into the order Isospondyli, an order first conceived by Cope (1871). However, Berg (1940) believed the Isospondyli to be an unnatural group, and erected the order Clupeiformes to include, among others, the Salmonidae. The order Clupeiformes is a grade, based on a combination of characters (Berg, 1940:417) many of which are now considered plesomorphic for teleosts

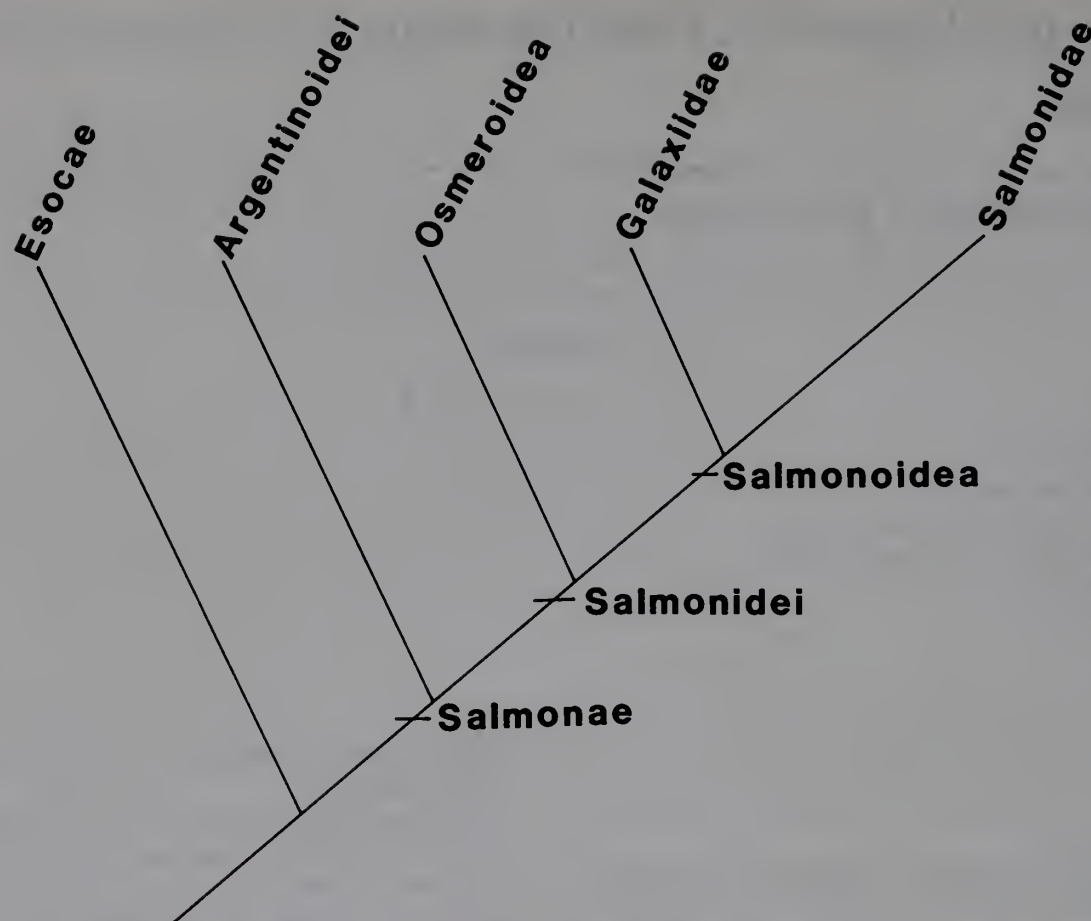


Fig. 1 Classification of salmoniform fishes (after Rosen, 1974).

(e.g. mesocoracoid usually present, scales usually cycloid). Indeed Berg states: 'This order ... represents an artificial assemblage.'

This idea persisted until Greenwood *et al.* (1966) redefined the Clupeiformes and created a division, Protacanthopterygii, which included four orders, one of which was Salmoniformes. This concept of Salmoniformes encompassed many taxa which have subsequently been removed (e.g. Stomiiformes, Myctophiformes, and Neoscolopelids; for a full summary see Lauder & Liem, 1983:132).

Rosen (1973, 1974) was the first author to consider the classification of the Salmoniformes in any detail, and this he did using a cladistic approach. He concluded that the Esocae, Argentinoidei, Osmeroidea, Galaxiidae and Salmonidae comprise the Salmoniformes (Fig. 1).

Fink & Weitzman (1982:85) and Fink (1984:205) considered the Salmoniformes a non-monophyletic group and hypothesized the Salmonidae to be the sister group to the Neoteleostei (Fig. 2).

Bonaparte (1832) originally used the family name Salmonidae, but did not list the included taxa. The three sub-families of the Salmonidae I recognise here: the Salmoninae, Thymallinae, and Coregoninae have been in a constant state of flux. Cope (1871, 1872) considered the Coregoninae a family, using the character of parietal bones meeting in the midline as justification. Gill (1893, 1895) incorrectly stated that the Coregoninae like *Salmo* have parietals that are separated by the supraoccipital, and thus elevated the third group of salmonids, the Thymallinae to family rank. This misobservation was corrected by Boulenger (1895) who stated there was '... no reason for separating *Coregonus* and *Thymallus* from the Salmonidae.'

The Thymallinae has been recognized as a family several

times (Jordan & Evermann, 1896; Tchernavin, 1923; and Berg, 1940).

More recently, Norden (1961) has provided a detailed osteological account of the Salmonidae which he recognised as comprising three subfamilies; Salmoninae, Thymallinae and Coregoninae. Both Norden (1961) and Behnke (1965:19) give detailed historical taxonomic accounts of the family.

Kendall & Behnke (1984) used external, larval and chromosome characters culled principally from published information to produce a cladistic analysis of the Salmonidae. From this analysis they recognised the Thymallinae as the sister-group to the Salmonidae and the Coregoninae the sister-group to those two (Fig. 3).

The most recent phylogenetic analysis of the Salmonidae is by Smith & Stearley (1989) whose paper was published after this text had been accepted for publication. These authors' results preempt to a certain extent those presented here and their cladograms of generic relationships, based on different and fewer morphological characters and on life-history characters supports the hypothesis of relationships set out here.

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## Materials and methods

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### Material

Specimens used for this study include those stored in alcohol, dry skeletons and cleared and double-stained specimens. All

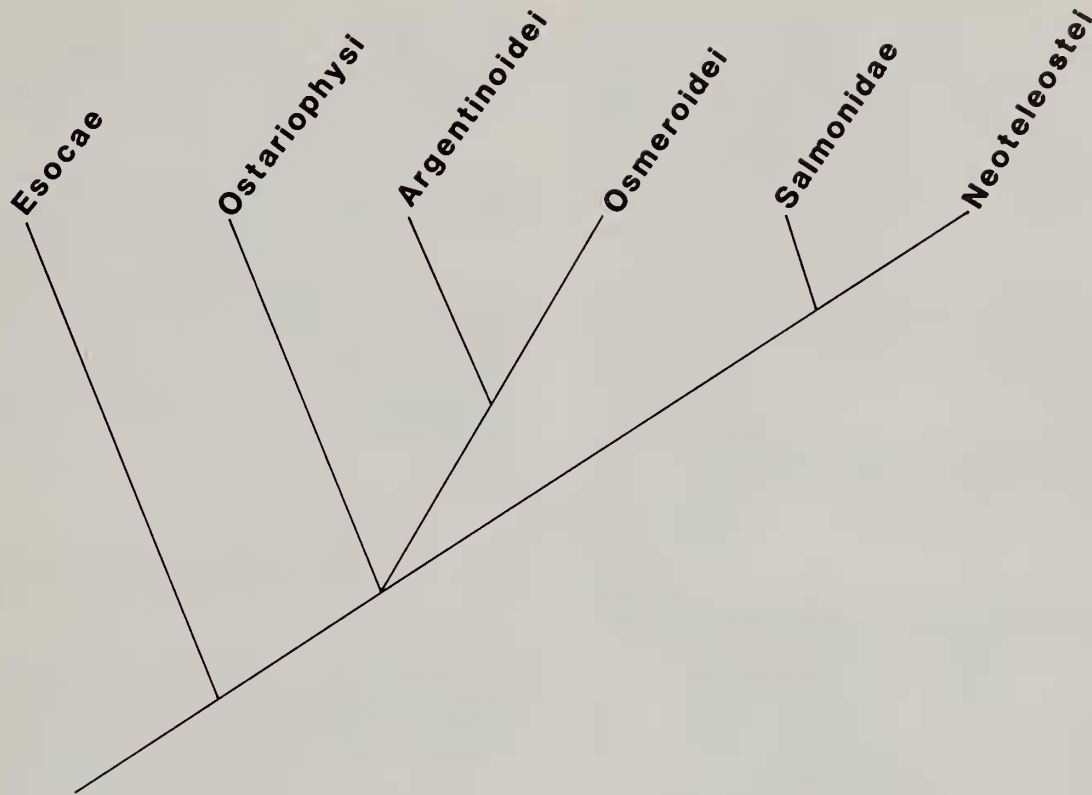


Fig. 2 Classification of 'lower' euteleostei (after Fink & Weitzman, 1982).

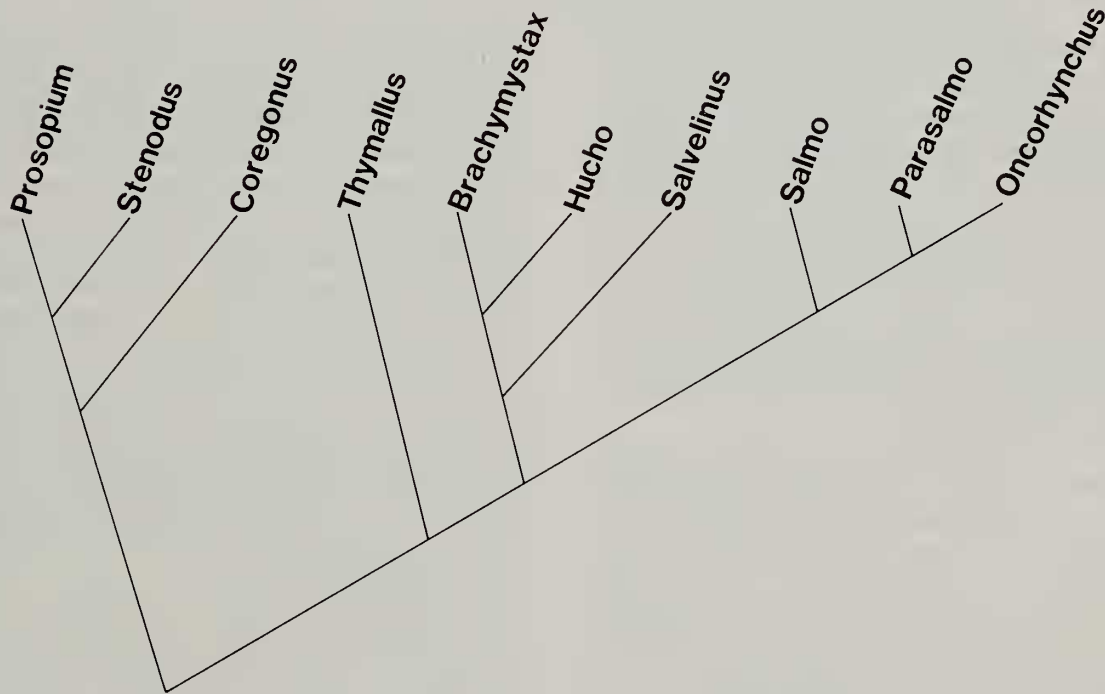


Fig. 3 Classification of salmonid genera (after Kendall & Behnke, 1984).

material used is held in the BMNH collections. A list of study taxa is give in Table I.

**NOMENCLATURAL NOTE.** Following recent recommendations of the American Society of Ichthyologists and Herpetologists Committee on Names of Fishes, the specific name of the rainbow trout used here is *mykiss* as distinct from the long-standing *gairdneri* (see Smith & Stearley, 1989 for discussion, and p. 151 below).

**Methods**

The intra- and interrelationships of the Salmonidae were evaluated using a cladistic analysis (*sensu* Nelson & Platnick, 1981; and Patterson, 1982). To establish those characters (homologies) which define monophyletic groups, knowledge of outgroup conditions is necessary (Patterson, 1982:51). The selection of 'appropriate' outgroups can be highly problematic (e.g. see Maddison *et al.* 1984) and is often based on

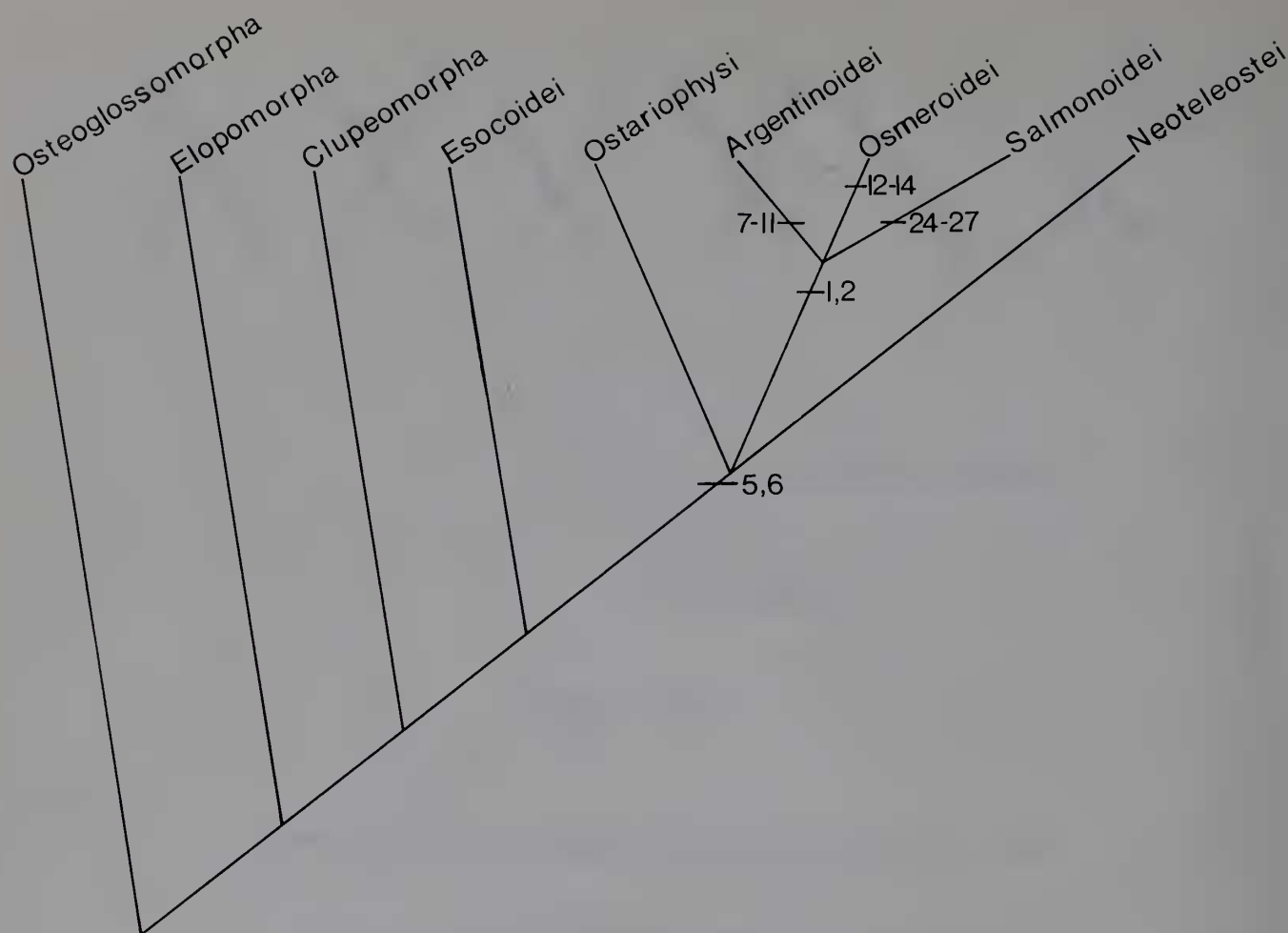


Fig. 4 Cladogram of salmonoid interrelationships. Characters enumerated in the text.

previous hypotheses of interrelationships. It is important to remember that outgroups do not necessarily possess plesiomorphic characters, as the very characters which define the taxon must, by implication, be autapomorphic. Thus, no single taxon can be assumed to be morphologically plesiomorphic for all characters.

In order to reduce the use of homoplastic characters in defining groups, a range of outgroup taxa was used, when possible, to examine the diversity of morphological configurations. As Stiassny (1986:414) points out 'Clearly it is not always the same taxon that bears the plesiomorphous state for each character under consideration.'

Another major criterion for establishing homology or the generality of a character, and thus relationships, is ontogeny (Nelson, 1978; and Patterson, 1982:52). Where possible this principle was employed to support decisions of character polarity, and thus hypotheses of relationships.

For the purposes of this study the Salmonidae (composed of the Salmoninae, Thymallinae and Coregoninae) and its included genera were considered the ingroup. The monophyly of the Salmonidae is based on a tetraploid karyotype (Gold, 1979:389). The first level of outgroup comparison (Unit I outgroup) was based on those taxa which Rosen (1974) included in the 'Salmoniformes'. Rosen's attempts at establishing monophyly of the 'Salmoniformes' have met harsh criticism (Fink & Weitzman, 1982; Lauder & Liem, 1983:132). Consequently, a second level of outgroup comparison (Unit II outgroups) has been used to minimize mistakes when making decisions of character polarity. This second level of comparison was aimed at a wide range of teleost fishes, from so-called 'primitive' groups (e.g.

osteoglossomorphs, elopomorphs and clupemorphs) to those which can be considered phylogenetically 'derived' (e.g. Stomiiformes, Paracanthopterygii and Acanthopterygii). For a list of taxa used in Unit I and Unit II outgroups, see Table I.

The dramatic morphological changes which some salmonids undergo when maturing have been well documented (Tchernavin, 1918, 1937, 1938b, and 1943); for example, hyperdevelopment of the ethmoid region, and loss of the teeth at certain developmental stages. While these changes can be important in formulating lower level taxonomic hypotheses; such modifications make comparison with outgroups rather problematic as no outgroup shows such extensive morphological changes. As pointed out by Nijhout *et al.*, (1986:455); 'Examining characters from earlier ontogenetic stages was also useful in that it allowed us to recognize homologous features prior to their concealment by subsequent differentiation.'

A taxonomic study of the Salmonidae requires a comprehensive review of their anatomy. As *Salmo salar* is the type species of the genus *Salmo*, a detailed account of the osteology of this species formed the basis for comparison with other salmonid taxa. The osteological characters utilized were of the ethmovomerine, anterior orbital, otic and occipital regions of the cranium; the jaws, hyopalatine, branchial and hyoid arches; opercular series; pectoral and pelvic girdles; vertebral column; dorsal, anal and caudal fin skeletons.

No complete morphological account of *Salmo salar* has been published and although Norden (1961) included Salmoninae in his osteological account, his descriptive emphasis was on Thymallinae. In contrast, the myology of other salmonids has been the subject of some attention. The

cranial and body musculature of *Oncorhynchus tshawytscha* has been described by Greene & Greene (1913), and the cranial myology of *Salvelinus fontinalis* was described by Lauder & Liem (1980). However, the myology of *Salmo salar* has not been discussed but was used in this study as the basis of comparison, first to other salmonids and secondly to outgroups.

In addition to cranial muscles, other characters involving ligaments of the ethmoid region; scales, nasal flaps and papillae, and breeding tubercles were used.

The osteological and myological descriptions with accompanying illustrations and relevant discussions determining character polarity which form the basis of the following hypotheses of interrelationships are not included here. These data are available as microfiche from Natural History Museum Publications.

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## Interrelationships of the Salmonidae

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The results of the character comparisons and analyses have revealed that the Salmonidae is a monophyletic group (see below under 'intrarelationshps'). The following hypothesis of interrelationships is summarized in Fig. 4.

The Salmonidae, Argentinoidei (*sensu* Greenwood & Rosen, 1971) and Osmeroidei (*sensu* Fink & Weitzman, 1982) together comprise a monophyletic group synonymous with Rosen's (1974) Salmonae, and are recognized by the following synapomorphies (the numbers preceding each character refer to their position in the cladogram, Fig. 4):

- 1) Absence of radii on scales
- 2) Well-developed teeth on the margin of the basihyal (independently derived in osteoglossomorphs, e.g. *Hiodon* and *Notopterus*)

The Salmonidae and Argentinoidei are united by the following synapomorphy:

- 3) Autogenous neural arches anterior to the dorsal fin. (considered to have been independently derived in some clupeomorphs)

The Osmeroidei and Argentinoidei are also united by an apparent homologous loss:

- 4) Absence of a maxillary-premaxillary ligament

Fink & Weitzman (1982:84) also suggest that fusion of the posterior neural arches with either the uroneural or first ural centrum is a condition uniting argentinoids and osmeroids but this appears to be of doubtful phylogenetic significance.

The relationships of the Salmonidae, Osmeroidei and Argentinoidei thus remain in doubt, and they are recognized as forming an unresolved trichotomy. Because in this proposed scheme of relationships the Salmonidae of previous authors (e.g. Norden, 1961) is ranked at the same taxonomic level as the suborders Osmeroidei and Argentinoidei, it is elevated to subordinal status, *viz.* Salmonoidei (Fig. 4).

The Salmonoidei, Osmeroidei and Argentinoidei (= Salmonae of Rosen, 1974) are considered to form one of the lineages of a second trichotomy comprising the Neoteleostei and the Ostariophysi. This hypothesis of relationships is based on two synapomorphies:

- 5) Loss of a toothplate over basibranchial 4 (also Lauder & Liem, 1983:134)

## 6) Fusion of the first preural and first ural centra

While I also agree with Fink & Weitzman (1982:85) that the Salmonoidei are one of the unresolved sister-groups of the Neoteleostei, I disagree that the two characters they use to propose this hypothesis are synapomorphic at this level. The first of these characters, a *tripartite occipital condyle* is, I believe, a homology of the Salmoninae, and is independently derived in neoteleosts, and some osteoglossomorphs (for discussion, see microfiche).

The second character used by Fink & Weitzman (*loc.cit*) is the presence of *rostral cartilages*. However, rostral cartilages have a more widespread distribution than given by these authors and are thus regarded as characters of little phylogenetic significance.

The following taxa can be defined by suites of autapomorphies, in addition to those used by Greenwood & Rosen (1971), Fink & Weitzman (1982) and Howes & Sanford (1987a, 1987b).

The Argentinoidei (*sensu* Greenwood & Rosen, 1971) comprising the superfamilies Argentinioidea and Alepocephaloidea:

- 7) Lateral displacement of the anterior foramen of the trigemino-facialis chamber
- 8) Fusion of the 1st, 2nd and 3rd supraneurals in Argentinioidea only
- 9) An extensive *dilatator opercularis* muscle originating in part from the hyomandibular
- 10) Presence in some alepocephaloids of an  $A_1$  division of the *adductor mandibulae* muscle
- 11) Absence of a maxillary-ethmoid ligament

Osmeroidei (*sensu* Fink & Weitzman, 1982) comprising the families Osmeridae and Galaxiidae:

- 12) Two foramina in the *pars jugularis*
- 13) A deep lamellate second uroneural
- 14) An open gutter-like preopercular canal

Galaxiidae (= Galaxiinae and Retropinninae). For the relationships of *Lovettia* and *Aplochiton* see Fink (1984):

- 15) Absence of a third uroneural
- 16) A low number of branched (principal) caudal fin rays
- 17) A double palatine-maxillary ligament
- 18) A double palatine-ethmoid cartilage ligament
- 19) Absence of a maxillary-ethmoid ligament

Osmeridae:

- 20) Formation of a semi-tubular ossification arising from the base of the *pars jugularis*

Esocae:

Esocidae:

*Esox*:

- 21) Expanded (antero-posteriorly) neural arches of the anterior region
- 22) Absence of a palatine-maxillary ligament

*Dallia*:

- 23) An ossified Baudelot's ligament

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## Intrarelationshps of the Salmonoidei

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As discussed under taxonomic history (p. 145) theories of the intrarelationshps of the Salmonoidei, like those of their

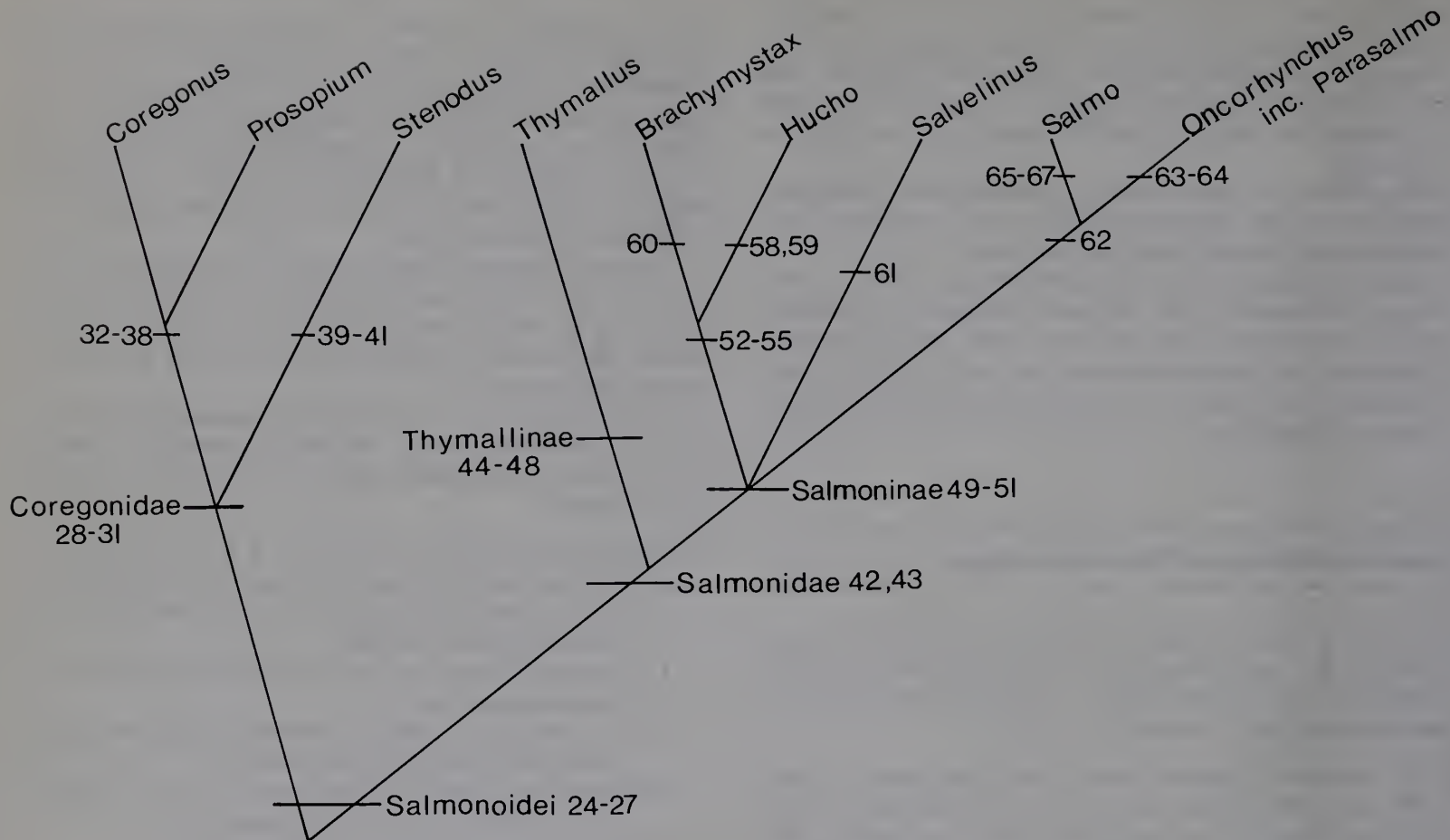


Fig. 5 Cladogram of salmonid intrarelationships. Characters enumerated in the text.

interrelationships, have been in a constant state of flux. This study has, however, revealed that the Salmonoidei (i.e. the Salmonidae *sensu* Norden, 1961; Fink, 1984; and Kendall & Behnke, 1984) are indeed monophyletic. The synapomorphies which define the Salmonoidei are:

- 24) Tetraploid karyotype
- 25) A deep posterior myodome, with the eye musculature passing through the myodome and attaching to the trunk muscles
- 26) A peg-and-socket arrangement of the posterior haemal arch elements of the caudal region
- 27) An anterodorsal process on the medial pelvic radial element

The suite of characters (homologies) listed below attest to the following hypothesized relationships, which are summarized as a cladogram (Fig. 5).

The Coregonidae (*Coregonus*, *Prosopium* and *Stenodus*) can be united on the following synapomorphies:

- 28) The presence of a dorsal flange in the posterodorsal region of the symplectic bone
- 29) A continuous articulation between the palatine and ethmoid cartilages
- 30) A short palatine bone
- 31) Absence of a palatine-premaxillary ligament

In contrast to the views of Kendall & Behnke (1984), who regard *Stenodus* and *Coregonus* as forming a monophyletic lineage with *Prosopium* as its sister-group, I consider *Coregonus* and *Prosopium* as a monophyletic group with *Stenodus* as its sister-group. Monophyly of *Coregonus* and *Prosopium* is supported by:

- 32) Presence of a separate supra- and rostrodermethmoid

- 33) Absence of vomerine teeth
- 34) A well-developed posterior myodome
- 35) An anteroventral process of the hyomandibular
- 36) Lack of any association between the palatine and maxilla
- 37) An expanded ventral region of the posttemporal bone
- 38) General absence of the ethmoid ligaments, in particular the maxillary-ethmoid ligament

Autapomorphic characters for *Stenodus* are:

- 39) A second flange on the lateral face of the hyomandibular bone
- 40) Absence of a medial strut on the mesocoracoid
- 41) Division of the  $A_2$  section of the *adductor mandibulae muscle* into  $A_{2a}$  and  $A_{2b}$

Characters establishing the Salmonidae (Thymallinae and Salmoninae as defined here) as a monophyletic assemblage are:

- 42) A well-developed 'palatine hook' where the cartilaginous region of the palatine forms a hook over the maxillary head
- 43) A reduced first proximal pterygiophore of the anal fin

Synapomorphic characters for the Thymallinae are:

- 44) A concave interface at the posterior symphysis of the pelvic basiptyrgia
- 45) Absence of an orbitosphenoid
- 46) The pattern of the latero-sensory canal in the last infraorbital
- 47) Papillae in the nasal region, between the nasal flaps

48) A minimum of 17 dorsal fin rays

Synapomorphies for the Salmoninae are:

49) Reduced parietal bones well separated by the supraoccipital

50) A tripartite occipital condyle

51) A suprapreoperculum

*Hucho* and *Brachymystax* have previously been united as a monophyletic group by Kendall & Behnke (1984), and I agree with this hypothesis on the basis of:

52) A single row of well-developed teeth along the head of the vomer

53) A plate-like flattened medial process of the post-temporal bone

54) A notch on the ventral surface of the medial proximal radial of the pelvic fin

55) Slender infraorbital bones

The genus *Salvelinus* has been united with *Hucho* and *Brachymystax* by Holčík (1982), on the basis of modified lateral line scales. However, examination of the lateral line scale reveals that there are no unusual features which indicate a close phylogenetic relationship between these three taxa. Despite this character negation, there is another possible synapomorphy which could be used to support Holčík's hypothesis:

56) An undivided border of the rostrum-dermethmo-supraethmoid

However, there is also a synapomorphy uniting *Salvelinus*, *Salmo* and *Oncorhynchus*:

57) The absence of a posteroventral process of the orbitosphenoid

In view of this character conflict *Salvelinus* is represented as one lineage of an unresolved trichotomy (Fig. 5).

Autapomorphic characters for *Hucho* are:

58) A reduced posttemporal fenestra

59) A truncate vertical shaft of the hyomandibular bone

Autapomorphic for *Brachymystax* is

60) A second flange in the posterior region of the hyomandibular bone

An automorphy for *Salvelinus* is:

61) A fragmented lateral extrascapular bone

As there are no autapomorphic characters indicating that *Cristivomer* (Gill & Jordan, 1878) should be regarded as a separate genus, it is here recognized as a synonym of *Salvelinus*. *Oncorhynchus* and *Salmo* are recognized as sister-groups on the basis of their having:

62) A well-developed vomerine shaft bearing well-developed teeth for its entire length

*Salmo* as presently defined (e.g. Norden, 1961), contains species from both Atlantic and Pacific waters. During the course of this study it has become clear that those *Salmo* species having their original distribution in the rivers of the western coastal region of north America should be included in the genus *Oncorhynchus* (see below).

Synapomorphies which define *Oncorhynchus* are:

63) The intercalar bone extends anteriorly to contact the prootic

64) The exoccipital bone has three foramina (*cf.* two in *Salmo*), the third being for the passage of the occipital nerve

This referral of the Pacific coast *Salmo* to *Oncorhynchus* was also proposed by Regan (1914). The Pacific coast *Salmo* species have also been regarded as constituting a separate subgenus (*Parasalmo* Vladykov, 1963). However, no synapomorphies have been discovered to indicate that the Pacific *Salmo* should be regarded as a group distinct from *Oncorhynchus* (see also Smith & Stearley, 1989).

It is interesting to note that recent analysis using protein electrophoretic techniques (e.g. Ferguson & Fleming, 1983; Berg & Ferris, 1984; and Johnson, 1984) has also indicated that the Pacific coast *Salmo* species are more closely related to *Oncorhynchus* than to the Atlantic coast *Salmo*.

*Salmo* can be defined on the basis of:

65) A pronounced notch in the anterior region of the ethmoid cartilage, and a well-developed 'kype' in the adult, where the lower jaw curves up and is accommodated by a large pocket in the roof of the mouth

66) An anterior, medially directed process of the metapterygoid

67) A truncate posterodorsal process on the operculum

As there are no autapomorphies indicating that *Salmothymus* (Berg, 1908) should be regarded as a separate genus, it is here recognized as a synonym of *Salmo*.

The above hypothesis of relationships, summarized as a cladogram (fig. 5), is presented in the following revised classificatory scheme:

Suborder Salmonoidei (new usage)

Family Coregonidae (new usage)

Subfamily Coregoninae (new usage)

Genus *Coregonus*

Genus *Prosopium*

Subfamily nov. *Stenodinae*

Genus *Stenodus*

Family Salmonidae (new usage)

Subfamily Thymallinae

Genus *Thymallus*

Subfamily Salmoninae

Genera *Hucho*

*Brachymystax*

*Salvelinus*

*Salmo*

*Oncorhynchus*

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## Proposed Changes in Taxonomic Ranking

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Because, in this proposed scheme of relationships the Coregoninae of previous authors (e.g. Norden, 1961), is ranked at the same taxonomic level as the family Salmonidae, it must be elevated to family status, *viz.* Coregonidae. In addition, the Salmonidae of previous authors (e.g. Norden, 1961; Kendall & Behnke, 1984) is here restricted to include the genera *Thymallus*, *Hucho*, *Brachymystax*, *Salvelinus*, *Salmo* and *Oncorhynchus*.

Taxonomic conclusions arrived at here support Smith & Stearley's (1989) adoption of the generic name *Oncorhynchus* for the Pacific basin species and *Salmo* for the Atlantic and Eurasian species of salmon.

Listed below are those species assigned to *Oncorhynchus*

and *Salmo* (based principally on Behnke, 1965); the validity of some species has yet to be ascertained.

*Oncorhynchus*: *aguabonita* Jordan, 1892; *apache* Miller, 1972; *chrysogaster* Needham & Gard, 1964; *clarki* Richardson, 1836; *gilae* Miller, 1950; *mykiss* Walbaum, 1792 (*gairdneri* Richardson is a synonym).

*Salmo*: *ischchan* Kessler, 1877; *obtusirostris* Heckel, 1852; *ohridanus* Steindachner, 1892; *pallaryi* Pellegrin, 1924; *platycephalus* Behnke, 1968; *salar* Linnaeus, 1758; *trutta* Linnaeus, 1758; *zetensis* Hadzisce, 1960.

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**Table I** List of taxa studied arranged in taxonomic categories (see text for explanation of outgroups).

SALMONIDAE: Coregoninae; *Coregonus albula*, *C. lavaretus*, *C. nasus*, *Prosopium cylindricus*, *P. williamsoni*, *Stenodus leucichthys*. Salmoninae; *Brachymystax lenok*, *Hucho hucho*, *H. perryi*, *H. taimen*, *Oncorhynchus clarki*, *O. gorbuscha*, *O. kisutch*, *O. masou*, *O. mykiss*, *O. nerka*, *O. tshawytscha*, *Salmo obtusirostris*, *S. salar*, *S. trutta*, *Salvelinus alpinus*, *S. fontinalis*, *S. malma*, *S. namaycusch*. Thymallinae; *Thymallus arcticus*, *T. brevirostris*, *T. thymallus*.

UNIT I OUTGROUPS: Argentinoidei; *Alepocephalus bairdi*, *A. rostratus*, *Argentina silus*, *A. sphyraena*, *Searsia koefoedi*. Escoidei; *Dallia pectoralis*, *Esox americanus*, *E. niger*, *Umbra krameri*, *U. pygmaea*. Galaxiidae and associated taxa; *Aplochiton zebra*, *Galaxias fasciatus*, *G. fontanus*, *G. maculatus*, *G. platei*, *Paragalaxias dissimilis*, *Prototroctes maraena*, *Retropinna retropinna*, *Stokellia stokellia*. Osmeridae and associated taxa; *Hypomesus olidus*, *Mallotus villosus*, *Osmerus esperlanus*, *O. mordax*, *Plecoglossus altivelis*.

UNIT II OUTGROUPS: Clupeomorpha; *Clupea harengus*, *Ethmalosa dorsalis*, *Etrumeus teres*, *Odaxothrissa lasera*, *Sardinella aurita*, *Sprattus sprattus*. Elopomorpha; *Albula vulpes*, *Elops* sp., *E. hawaiiensis*, *E. machnata*, *Megalops cyprinoides*. Neoteleostei; *Dicentrarchus labrax*, *Gadus morhua*, *Lepomis macrochirus*, *Maurollicus mulleri*, *Merluccius merluccius*, *Normanichthys crockeri*, *Pollichthys mauili*, *Saurida gracilis*, *Synodus foetens*. Ostariophysii; *Alestes dentex*, *Chanos chanos*, Osteoglossomorpha; *Hiodon alosoides*, *Osteoglossum bicirrhosum*, *Scleropages formosus*, *S. leichhardtii*.